Deep-Sea Research I 72 (2013) 9–16

Contents lists available at SciVerse ScienceDirect

Deep-Sea Research I

journal homepage: www.elsevier.com/locate/dsri

Vertical migration and diel feeding periodicity of the skinnycheek lanternfish (*Benthosema pterotum*) in the Red Sea

Eivind Dypvik*, Stein Kaartvedt

Red Sea Research Center, 4700 King Abdullah University of Science and Technology, Thuwal 23955-6900, Saudi Arabia

ARTICLE INFO

Article history:
Received 19 June 2012
Received in revised form
11 October 2012
Accepted 18 October 2012
Available online 13 November 2012

Keywords:
Benthosema pterotum
Skinnycheek lanternfish
Acoustic scattering layers
Diel vertical migration
Feeding periodicity

ABSTRACT

The vertical migration and diel feeding periodicity of the skinnycheek lanternfish (*Benthosema pterotum*) were studied by use of a hull-mounted 38 kHz echo sounder, ROV-deployments and net-sampling at two locations (~24°48′N, ~36°15′E and ~21°27′N, ~38°5′E) in the central Red Sea. The mesopelagic zone of the Red Sea represents an unusual environment with very high temperatures (~22 °C) and low zooplankton concentrations (< 10 individuals m^{-3} below 600 m). The skinnycheek lanternfish performed normal diel vertical migration from ~500 to 750 m during daytime to the epipelagic zone (upper ~200 m) at night. A strict feeding periodicity occurred; with the skinnycheek lanternfish foraging on zooplankton throughout the night, while rapidly digesting the preceding nocturnal meal in the warm mesopelagic region. We hypothesize that the constrained epipelagic distribution of zooplankton and the unusual warm waters of the Red Sea force the whole population to ascend and feed in epipelagic waters every night, as the prey-ration eaten each night is fully digested at mesopelagic depths during daytime.

1. Introduction

The mesopelagic zone at ~200–1000 m depth is defined as the part of the water column with too little light for photosynthesis, but sufficient downwelling irradiance for visual detection of prey (Robinson et al., 2010). Lanternfishes (Myctophidae) are zooplanktivorous mesopelagic fish distributed in the mesopelagic zone of all the world's oceans (Kinzer and Schulz, 1985; Dalpadado, 1988; Moku et al., 2000; Cherel et al., 2010). They form acoustic backscattering layers (SL's) and their behavior have often been studied through traditional sampling methods such as trawling combined with acoustic surveys (Gjøsæter, 1984; Valinassab et al., 2007; Collins et al., 2008; Godø et al., 2009; Kaartvedt et al., 2009).

Lanternfishes are assumed to be important contributors to the biological pump (Hernandez-Leon et al., 2010), bringing organic materials from the epipelagic to the mesopelagic zone as they perform normal diel vertical migrations (NDVM), feeding in surface layers at night and excreting while hiding from visual predators at mesopelagic depths during the day (Clarke, 1978; Giske et al., 1990; Robison, 2003; Collins et al., 2012). However, in most oceans, parts of the lanternfish population perform no diel vertical migrations (NoDVM) or inverse diel vertical migrations (IDVM), residing, feeding and spawning in the mesopelagic zone (Gjøsæter and Tilseth, 1988; Moku et al., 2000; Collins et al., 2008; Olivar et al., 2012; Dypvik et al., 2012a,b). In contrast to this pattern, a recent study in the Red Sea indicated that >95% of the mesopelagic fish, including the skinnycheek lanternfish (*Benthosema pterotum*) which is the dominant lanternfish in the Red Sea (Dalpadado and Gjøsæter, 1987), performed NDVM from the mesopelagic zone to the upper ~200 m at night (Klevjer et al., 2012). The authors suggested that low feeding opportunities due to very low zooplankton concentrations (Weikert, 1982; Böttger-Schnack, 1990; Böttger-Schnack et al., 2008) and rapid digestion in the very warm waters at mesopelagic depths in the Red Sea, forced the entire population of mesopelagic fish to carry out nocturnal feeding migrations to upper layers every night (Klevjer et al., 2012). However, no data on zooplankton or feeding were available in that study.

Previous studies have showed that the skinnycheek lanternfish forage on zooplankton in the upper ~200 m at night (Dalpadado and Gjøsæter, 1987), and reside below 350 m during the day (Thiel, 1979; Dalpadado and Gjøsæter, 1987). However, skinnycheek lanternfish have also been found to stay in the mesopelagic zone throughout day and night (Gjøsæter, 1984). In this paper, we examine the DVM pattern and feeding periodicity of the skinnycheek lanternfish in the Red Sea by utilizing echo sounders, net sampling and ROV-deployments to address the hypothesis that low prey concentration restricting feeding activity in the mesopelagic zone coupled with high digestion rates in the warm

* Corresponding author. Tel.: +966 544 701 841.
E-mail addresses: eivind.dypvik@kaust.edu.sa (E. Dypvik), stein.kaartvedt@kaust.edu.sa (S. Kaartvedt).

0967-0637
http://dx.doi.org/10.1016/j.dsr.2012.10.012

waters (as illustrated in Shreeve et al., 2009) force the whole population to ascend into the more plankton-rich epipelagic layer to feed at night.

2. Materials and methods

This study was conducted from 8 to 17 November 2011at two locations (~24°48′N, ~36°15′E and ~21°27′N, ~38°5′E) in the Red Sea (Fig. 1), using the R/V "Aegaeo". The two study sites were located at the Kebrit and Atlantis II deep sea brines, where bottom depths were ~1500 m and ~2200 m, respectively (see Antunes et al., 2011).

Temperature was measured using a CTD (Conductivity, Temperature, Depth; SD204-model, SAIV A/S) attached to a multinet used for zooplankton sampling (see below). Oxygen data presented in this study were obtained earlier in the cruise (Atlantis II (26 Sep. 2011) and Kebrit (1 Oct. 2011)), using a SeaBird CTD equipped with a SeaBird oxygen sensor.

Zooplankton were sampled day (between sunrise and sunset) and night (between sunset and sunrise) using a multinet (MPS Mini Combi, HYDRO-BIOS) with five nets of 200 μm mesh size, and a net opening of 0.125 m^2. The nets could be opened and closed remotely, permitting depth stratified sampling. At the Kebrit station, one day-series and one night-series were sampled in nine depth intervals (0–1460 m). However, the day-series from Kebrit was excluded from the analysis, since some of the samples were inadvertently filtered through a 500 μm sieve. At the Atlantis II station, two day-series and two night-series were sampled in nine depth intervals (0–2000 m). Samples were fixed in 4% formalin for later identification and numeration.

Sampling for fish was conducted throughout the 24-h cycle, targeting the depths of different SL's (see "Results"; "Identification of SL's"), with a Hamburg plankton net (HYDRO-BIOS) with 500 μm mesh size and a 7 m^2 mouth opening. Sampling depths of the oblique tows were monitored using a Scanmar depth sensor. The cruising speed while trawling was ~2 knots and the trawl-time varied from 10 to 90 min, depending on strength of acoustic backscatter at the sampling depth. The Hamburg net had no mechanism facilitating remote opening and closing. Thus, in order to minimize by-catch from the descent and ascent to the desired sampling depth, vessel speed was reduced during deployment and retrieval of the net. Thirty-nine successful tows were conducted, 13 at Kebrit (6 day and 7 night tows) and 26 at Atlantis II (7 day and 19 night tows). Upon recovery of the net, fish were separated from the rest of the catch and frozen for later analysis.

A total of 310 skinnycheek lanternfish were caught and analyzed for stomach contents and size. Of these, only two had regurgitated stomachs and were disregarded. The standard length was recorded for each individual, and the stomachs were removed as described by Sameoto (1988, 1989). A stereo microscope (10× and 40× magnification) was used for the analysis of stomach content. The degree of stomach fullness and digestion were categorized from 1 to 5 (1: empty, 5: full/distended for fullness; 1: fresh, 5: fully digested/unrecognizable for digestion (Fotland et al., 2000)) and stomach contents were identified to nearest possible taxon, with increasing uncertainty with the degree of digestion. Diel variability in the stomach content of the skinnycheek lanternfish was explored statistically using Kruskal–Wallis tests and Tukey post-hoc analysis, using the IBM SPSS Statistics software.

Acoustic data were collected with a calibrated hull-mounted Simrad EK60 (ES38) 38-kHz split-beam echo sounder, with a 7° beam angle. The echo sounder was continuously transmitting at a rate of 0.4 ping s^{-1}, except during periods when the echo sounder was interfering with short-term use of other acoustic instruments. The acoustic data was filtered to remove acoustic noise (see Klevjer et al., 2012 for further description), and then presented as 24-h echograms. Matlab and LSSS (Korneliussen et al., 2009) were used for acoustic data processing and illustrations.

A remotely operated vehicle (ROV) equipped with a macro-zoom and two wide-angle cameras (see Batang et al., 2012 for further description) was deployed during daytime at Kebrit (three deployments) and around sunset at Atlantis II (one deployment). The ROV descended towards the bottom at a rate of ~0.4 m/s while the cameras recorded continuously. During one daytime deployment, the lights were turned off as the ROV descended, then turned on for five-minute periods when the ROV stopped within the different SL's. Few fish were observed during this deployment, thus, during the other deployments, the lights were on continuously. The videos were analyzed for presence of fish by counting skinnycheek lanternfish observed in hundred meter depth intervals. The skinnycheek lanternfish was identified based on its morphology and a characteristic stop-and-go swimming pattern, corresponding to that observed from submersibles (Barham, 1966) and recorded acoustically (Kaartvedt et al., 2008) in other lanternfish species. Some individuals were probably counted at least twice as they would disappear from the field of view of the camera, but reappear later. However, these results are merely used to complement the net-tow data and the acoustic data on the vertical distribution of the skinnycheek lanternfish. Thus, the depth where the skinnycheek lanternfish first appear is of most importance.

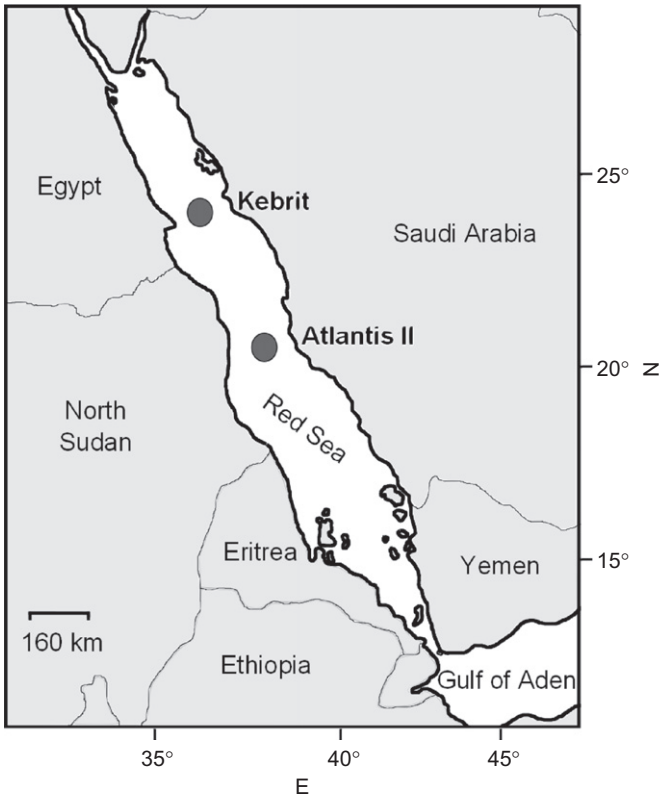

Fig. 1. Map of the Red Sea. Kebrit and Atlantis II are marked with dark gray circles.

3. Results

3.1. Hydrography

At both stations, the temperature decreased from >26 °C at the surface, converging to ~22 °C at ~250 m (Fig. 2). The oxygen

levels decreased from ~4.5 ml O_2 l^{-1} in the surface to an oxygen minimum zone with oxygen levels < 1.5 ml O_2 l^{-1} between ~300 and 750 m at Atlantis II and ~400–750 m at Kebrit (Fig. 2). Below ~750 m, the oxygen levels increased towards ~2 ml O_2 l^{-1} (Fig. 2).

3.2. Zooplankton distribution

Zooplankton was mainly distributed in the upper 100–200 m of the water column at Kebrit and Atlantis II, with very low concentrations at mesopelagic depths (Table 1). The ratio of zooplankton in the upper 200 m versus zooplankton deeper than 200 m was > 25 at both stations and total number of zooplankton below 600 m was < 6 individuals m^{-3} (Table 1). ~80% of the zooplankton were copepods, with calanoid copepods and cyclopoid copepods being the most numerous overall taxa (Table 1).

3.3. Acoustic records

Four different SL's were visible during daytime at both stations; two shallow SL's were distributed at ~100 m (SL1) and ~200 m (SL2), one SL (SL3) was distributed at ~350–550 m, while the deepest SL (SL4) was distributed at ~600–750 m (Fig. 3). SL1 seemed to consist of non-migrators, while the other SL's consisted of normal diel vertical migrators, with the whole population taking part in the migrations.

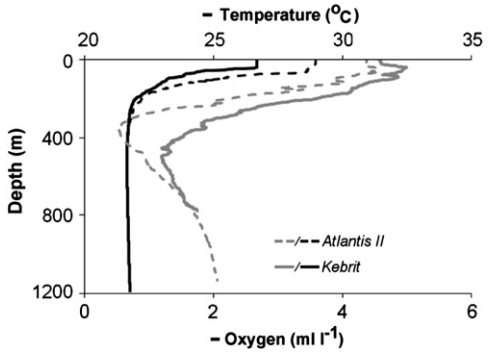

Fig. 2. Temperature (black) and oxygen (gray) measured at Kebrit (continuous line) and Atlantis II (dotted line).

Results from one diel cycle are presented in Fig. 3, but similar patterns were observed throughout the cruise and at both stations. About 1 h prior to sunset (~16:30), individuals in the SL's began their ascent towards the upper 200 m, where they remained until beginning their descent back to daytime depths ~1 h prior to sunrise (~05:40) (Fig. 3). No SL's were visible below ~200 m at night (Fig. 3).

3.4. Identification of SL's

In net-tows directed towards SL1-3 during daytime, *Vinciguerria mabahiss* was the dominant mesopelagic fish, while no skinnycheek lanternfish were caught at these depths (Fig. 4). However, skinnycheek lanternfish were observed in the ROV-videos at depths corresponding to the lower part of SL3 (Figs. 3 and 5a). Skinnycheek lanternfish were caught in net-tows directed towards SL4 during daytime (Fig. 4). Also, at the depths of SL4 observations of skinnycheek lanternfish in the daytime ROV-videos increased in frequency (Fig. 5a). When sampling was conducted below SL4, at depths with no apparent SL's, skinnycheek lanternfish were still caught (Fig. 4). In addition, a few codlets (*Bregmaceros* sp.) were caught in the deepest tows.

Individuals in SL3 (lower part) and SL4 seemed attracted to the light of the ROV, as they descended alongside the ROV deeper than their normal daytime depth range before returning to their normal daytime depth afterwards (Fig. 6). Corresponding ROV-observations of skinnycheek lanternfish were made below ~800 m during daytime (Fig. 5a).

The ROV deployed approximately at sunset recorded skinnycheek lanternfish from ~200–300 m (~18:00), peaking in recorded specimens at ~400–500 m (Fig. 5b). At this time, the SL3 and SL4 were ascending, and distributed at ~100–300 m and ~300–400 m, respectively (Fig. 3). In addition to the skinnycheek lanternfish, some unidentified fish species were also detected in the ROV-recordings.

During the night, most sampling was conducted in the upper ~200 m (Fig. 4). The skinnycheek lanternfish was present in all

Table 1
Zooplankton distribution at Kebrit (Night) and AtlantisII (Day/Night). Catches are illustrated as individuals m^{-3}. Average catches are given from Atlantis II, while the day-series from Kebrit is excluded. Chaetognatha, decapoda-larvae, amphipoda, medusa, polychaeta, appendicularia, nauplii, fish larvae, eggs and isopods are included in the group others.

Depth (m)	Calanoid cop.	Cyclopoid cop.	Poecilostomatoid cop.	Harpacticoid cop.	Ostracoda	Gastropoda	Others	Total
Kebrit (Night)								
0–50	220	58	58	1	1	15	73	427
50–100	310	53	40	1	13	16	59	492
100–200	25	26	2	< 1	7	< 1	10	70
200–400	12	12	0	0	3	< 1	4	31
400–600	7	4	< 1	< 1	4	< 1	2	17
600–800	4	1	< 1	0	< 1	< 1	1	6
800–1000	2	0	< 1	0	1	0	< 1	4
1000–1400	1	< 1	< 1	0	< 1	< 1	< 1	2
1400–1460	5	1	< 1	0	< 1	0	3	10
Atlantis II (Day/Night)								
Depth (m)								
0–50	395/325	155/111	73/58	6/10	3/6	22/21	97/93	751/624
50–100	161/158	67/55	51/47	2/1	9/17	2/5	39/49	331/332
100–200	34/19	15/14	4/4	1/3	3/5	< 1/1	8/11	65/57
200–400	19/16	5/7	1/2	4/4	5/3	< 1/< 1	3/4	37/36
400–600	8/8	4/7	1/2	1/1	3/3	0/< 1	1/2	18/23
600–1000	2/3	1/1	< 1/< 1	< 1/< 1	1/1	0/< 1	< 1/1	5/6
1000–1400	< 1/1	< 1/< 1	< 1/< 1	< 1/< 1	< 1/< 1	< 1/< 1	< 1/< 1	1/2
1400–1900	1/< 1	< 1/< 1	< 1/< 1	< 1/< 1	< 1/< 1	< 1/< 1	< 1/< 1	2/1
1900–2000	4/7	4/3	1/3	1/< 1	< 1/0	0/0	1/1	11/14

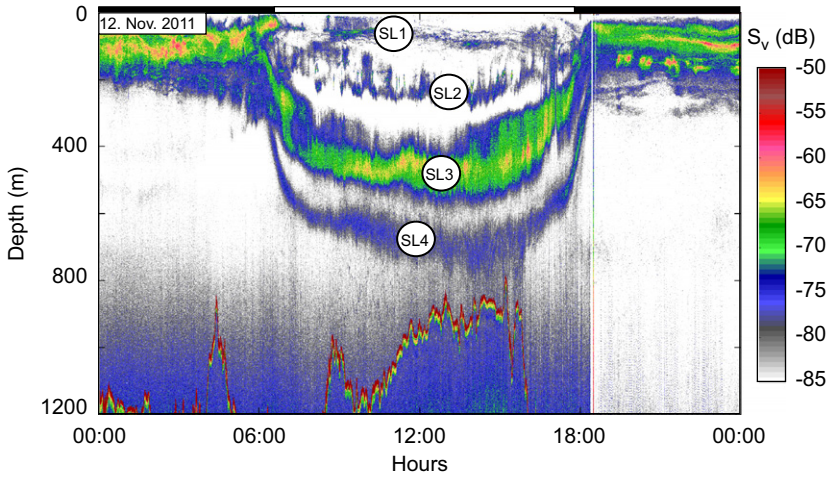

Fig. 3. 24-h echogram from the hull-mounted 38 kHz echo sounder on 12 November 2011. Different scattering layers are annotated. The coloration in the echogram refers to volume backscattering (S_v), where red illustrates the strongest and white the weakest backscatter. Black and white bars above the echogram depict night and day, separated by time for sunrise and sunset. Time is given as local time (UTC +3 h).

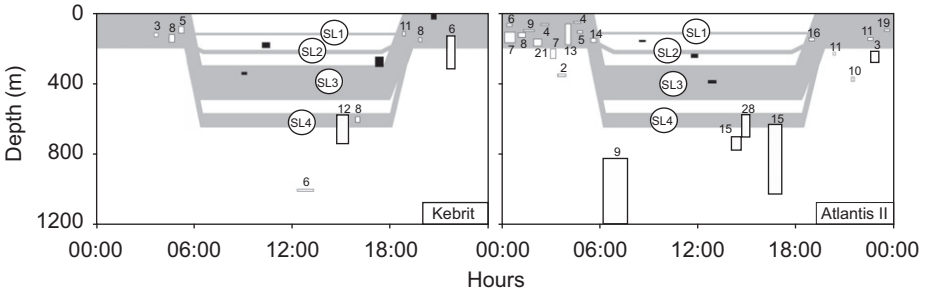

Fig. 4. Schematic presentation of trawl-hauls conducted at Kebrit and Atlantis II. Each box indicates the time of trawling (horizontally) and the depth of trawling (vertically). The white boxes indicate that skinnycheek lanternfish were caught, the number of individuals are marked. The black boxes indicate no catch of the skinnycheek lanternfish. The grey areas illustrate the approximate distribution of the scattering layers (see Fig. 3). Depth is not the max depth at each location, but merely set to 1200 m since no trawling was conducted, and no apparent backscattering appeared, below these depths. Time is given as local time (UTC +3 h).

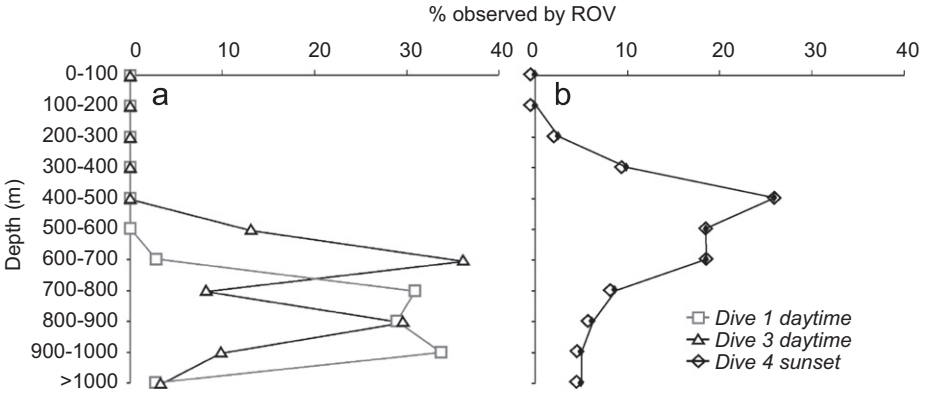

Fig. 5. The relative frequency (%) of all observed skinnycheek lanternfish in ROV-recordings in different depth intervals during day (Dive 1 and 3) at Kebrit (a) and ~sunset (Dive 4) at AtlantisII (b). n=106 during Dive 1, n=61 during Dive 3 and n=85 during Dive 4. Dive 2 was excluded from the figure, as only 2 skinnycheek lanternfish were observed (at ~650 m and ~900 m) during this dive.

these catches, except in the shallowest tow in the upper 25 m (Fig. 4). Some sampling was conducted below the SL, deeper than 200 m at night, and a few specimens of skinnycheek lanternfish were caught in these tows (Figs. 3 and 4).

A total of 309 individuals of skinnycheek lanternfish were measured for standard length. The smallest individuals were 0.9 cm, while the largest individual was 4.5 cm, and the average standard length was 1.94 cm.

3.5. Dietary analysis

The majority of the analyzed skinnycheek lanternfish (~60%) had identifiable stomach content (Fig. 7a), and ~43% of the individuals with identifiable stomach content contained more than one prey. The three most common groups of prey were calanoid copepods (~42%), ostracods (~19%) and gastropods (~14%) (Fig. 7b). Of the calanoid copepods found in the stomachs,

Pleuromamma sp. accounted for the majority (~58%). Macrozooplankton such as krill and amphipods were identified in 6.2% and 1.6% of the stomachs, respectively. Other prey included poecilostomatoid copepods, harpacticoid copepods, unidentified copepods, cyclopoid copepods, decapod larvae and isopods (Fig. 7b).

The skinnycheek lanternfish had significantly less stomach contents during day than night (Kruskall–Wallis, $p \ll 0.001$) and 84% of the dissected skinnycheek lanternfish caught during daylight-hours had empty stomachs. The proportion of individuals with prey in their stomach decreased and the degree of digestion increased from early daylight hours towards sunset (Figs. 8a,c and 9a,c), although there was no statistically significant differences in the amount of prey in stomachs of fish caught between different daylight hours (Kruskall–Wallis, $p=0.054$).

At night, 76% of all the dissected skinnycheek lanternfish had prey in their stomachs, and there were significant differences in amount of stomach content between night-hours (Kruskall–Wallis, $p=0.01$). Of the fish caught at night, least prey were recorded early at night (18:00–19:00) while most prey were recorded in stomachs of fish caught late at night (04:00–05:00 and 05:00–06:00). The exception from this trend was little stomach contents among fish caught at 01:00–02:00. Fish caught between 04:00 and 05:00 had eaten significantly more than fish caught between 18:00 and 19:00 (posthoc, Tukey test, $p=0.006$), 19:00–20:00 (posthoc, Tukey test, $p=0.026$) and 01:00–02:00 (posthoc, Tukey test, $p=0.002$), while fish caught between 05:00 and 06:00 had eaten significantly more than fish caught between 18:00 and 19:00 (posthoc, Tukey test, $p=0.022$) and 01:00–02:00 (posthoc, Tukey test, $p=0.04$). In the last night tow, 100% of the fish ($n=9$) had food in their stomachs, although these fish caught during the last hour before sunrise in total contained less prey in their stomach content, had less stomach fullness and higher degree of digestion than previous hours (Fig. 9a–c).

In sum, the amount of prey in stomachs increased from sunset to sunrise (Figs. 8a and 9a), and the stomach fullness and degree of digestion changed accordingly; more full stomachs and fresher stomach content towards sunrise (Figs. 8b–c and 9b–c). Stomach contents were digested and stomachs largely became empty in the course of the day (Figs. 8a–c and 9a–c).

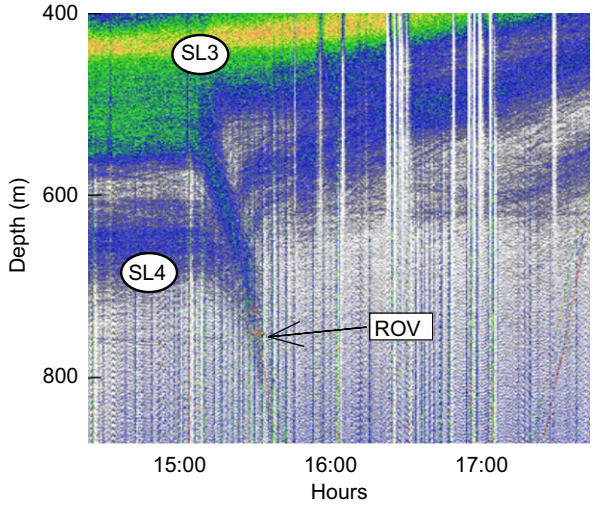

Fig. 6. Echogram from 11 November 2011 illustrating the attraction of organisms in SL3 and SL4 towards the descending ROV. The coloration in echograms refers to volume backscattering (S_v), where red illustrates the strongest and white the weakest backscatter. The S_v-threshold is set to −85 dB (scale is presented in Fig. 2). Time is given as local time (UTC +3 h).

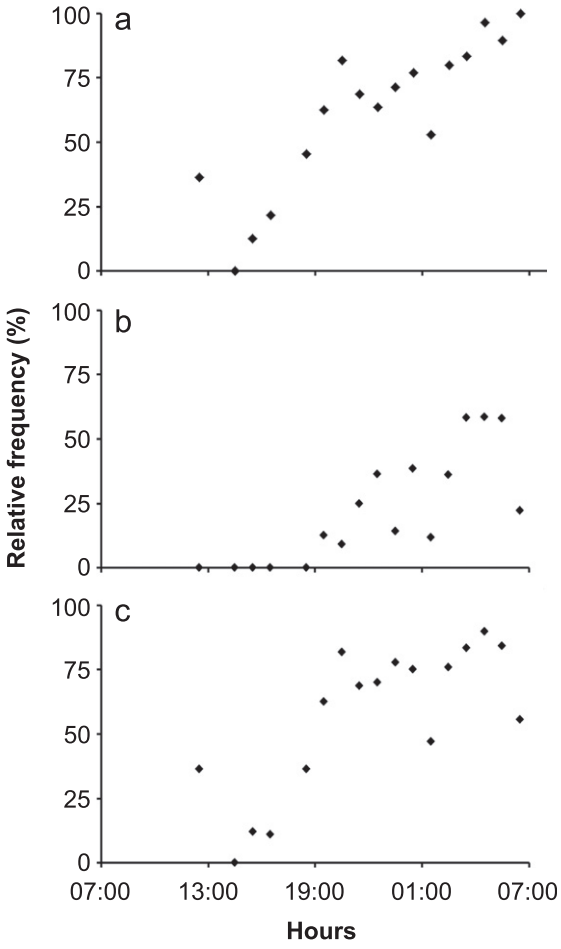

Fig. 8. Percentage of skinnycheek lanternfish caught at specific hours with prey in their stomachs (a), stomach fullness of category 4 or 5 (b), and degree of digestion of category 1–3 (c). Time intervals with no marking indicate no catch or no trawling (see Fig. 9 for details). The amount of fish analyzed per time interval (n) is given in Fig. 9. The time is set to start at 07:00 (local time), since this this is the first hour after sunrise.

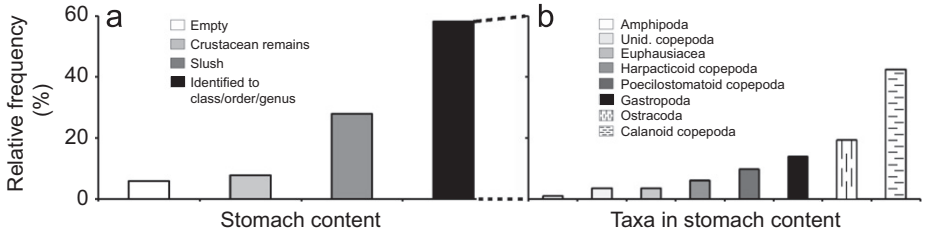

Fig. 7. Stomach content of the skinnycheek lanternfish. (a) Percentage of empty stomachs and different types of stomach contents in dissected skinnycheek lanternfish, $n=307$. (b) Identified prey allocated to taxa, $n=727$. Isopoda (0.1%), decapoda larvae (0.6%) and cyclopoid copepods (0.8%) are not included in figure (b).

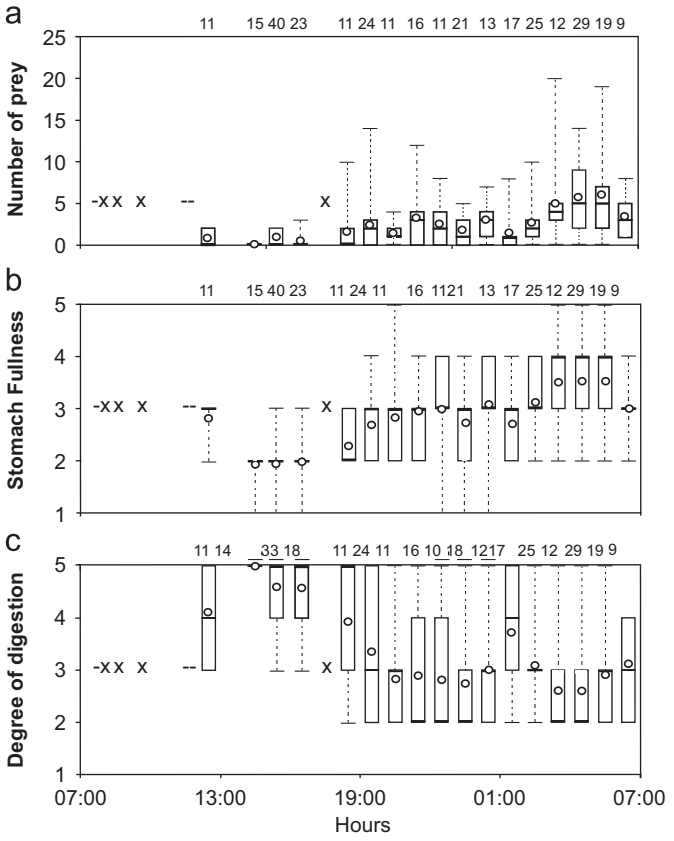

Fig. 9. Stomach content of the skinnycheek lanternfish at different times of day. (a) the number of prey in stomach contents at different hours; (b) degree of stomach fullness at different hours; (c) degree of digestion of stomach contents at different hours. The horizontal axis on top of figure depicts number of skinnycheek lanternfish analyzed for each time interval. The boxes illustrate the 25% quartile, the 50% median and the 75% quartile. The dotted lines illustrate the maximum and minimum value registered of prey (a), stomach fullness (b) and degree of digestion (c). The rings mark the average values. *x* indicate no catch and—indicate no trawling. The time is set to start at 07:00 (local time), since this this is the first hour after sunrise.

4. Discussion

The Red Sea population of skinnycheek lanternfish performed NDVM from the mesopelagic zone towards the surface at night and a strict diel feeding periodicity occurred. Little or no feeding was apparent during daylight-hours, while feeding on zooplankton took place throughout the night.

Multiple lines of evidence suggest that skinnycheek lanternfish spend the daylight hours at mesopelagic depths. Catches of the skinnycheek lanternfish in nets, acoustic data from a hull-mounted echo sounder, and video recordings from a ROV showed that skinnycheek lanternfish mainly occur in the deepest scattering layers (lower part of SL3 and SL4) of the Red Sea during daylight hours. Such a depth distribution is accordance with Thiel (1979) and Klevjer et al. (2012), but deeper than that observed by Dalpadado and Gjøsæter (1987). Skinnycheek lanternfish were also caught in trawl hauls below the deepest SL's, depth intervals with minimal backscatter, during day and night, suggesting that fish were caught during the ascent/descent of the trawl.

Klevjer et al. (2012) observed lanternfish in SL3 that became attracted to their manned submersible, as also found for lanternfish in other oceans (Barham, 1966). The acoustic data in the current study indicate that the backscattering organisms in the lower part of SL3 and in SL4 were attracted to the light of the ROV. These recordings were excluded as potential turbulence from the ROV, as attracted individuals continued their afternoon ascent after a while, and this pattern was not evident above or below the SL's in focus. Thus, the ROV-observations of skinnycheek lanternfish deeper than SL4 may be an artifact of light attraction. Regardless, we conclude that basically the whole population carries out DVM.

The net-catches of the skinnycheek lanternfish and other mesopelagic fishes were very low relative to the considerable sampling effort. This may be due to efficient avoidance of the Hamburg net as the ROV-recordings and the strength of the acoustic backscatter indicate that lanternfishes were common. Additionally, the average size of Red Sea skinnycheek lanternfish caught in a larger trawl by Dalpadado and Gjøsæter (1987) was >2 cm (standard length) larger than that of the current study, consistent with the larger individuals avoiding the Hamburg net. This is in accordance with Kaartvedt et al. (2012), who concluded that net sampling seriously underestimates the abundance of mesopelagic fish due to their efficient avoidance behavior. Alternatively, there may be a difference in size-structure between the population investigated in the current study and the population sampled by Dalpadado and Gjøsæter (1987). However, individuals caught in this study and observations of skinnycheek lanternfish in ROV-recordings are merely used to verify their presence in SL's, and particularly to study the feeding cycle of the skinnycheek lanternfish, for which the data proved appropriate.

During autumn, the whole population of skinnycheek lanternfish performed NDVM into the upper ~200 m at night. Acoustic records from spring showed the same DVM pattern (Klevjer et al., 2012), suggesting that this is a persistent pattern in the Red Sea. NDVM is a common behavioral pattern for lanternfishes (Kinzer and Schulz, 1985; Dalpadado and Gjøsæter, 1987; Collins et al., 2008), usually associated with nighttime feeding on zooplankton and daytime hiding from visual predators (Clarke, 1978; Kinzer and Schulz, 1985; Catul et al., 2010). In contrast to the skinnycheek lanternfish in the Red Sea, lanternfish populations in more productive, less extreme environments often display more diverse migration patterns, including NoDVM and IDVM (Pearcy et al., 1979; Shreeve et al., 2009; Dypvik et al., 2012b). Factors such as prey abundance, temperature, and oxygen levels may cause these behavioral differences (discussed further below).

The skinnycheek lanternfish had an opportunistic zooplankton based diet, dominated by calanoid copepods and ostracods. This is in accordance with previous studies of lanternfish species elsewhere (Kinzer and Schulz, 1985,; Dalpadado and Gjøsæter, 1988; Pakhomov et al., 1996; Pusch et al., 2004). Few of our studied individuals had fed on comparably larger, more nutritious macrozooplankton, such as krill and amphipods, which are important prey for lanternfishes in other areas (Pearcy et al., 1979; Williams et al., 2001; Shreeve et al., 2009). Dalpadado and Gjøsæter (1987) studied larger individuals of skinnycheek lanternfish than those in the current study. Although copepods remained as the primary prey of the adult population, euphausiids increased in dietary importance as individuals grew larger (Dalpadado and Gjøsæter, 1987). Thus, as previously reported in other lanternfish species (Roe and Badcock, 1984; Pusch et al., 2004; Shreeve et al., 2009), the skinnycheek lanternfish appears to have a size dependent diet.

The skinnycheek lanternfish had a strict daily feeding cycle. During night, stomachs of skinnycheek lanternfish contained freshly ingested prey; during daytime, they were empty or contained well digested, unidentifiable, prey. The digestion time in mesopelagic fish is not well known, but in accordance with previous studies, we interpret a low degree of stomach content digestion as recent feeding (Clarke, 1978; Dalpadado and Gjøsæter, 1988; Sameoto, 1989). We are confident that the observed daily feeding cycle is not influenced by net-feeding or regurgitation. Due to the stress of being captured by a trawl, feeding in the net by lanternfishes is not likely, however, regurgitation of food might

occur (Baird et al., 1975). Two individuals with regurgitated stomachs were easily distinguished and excluded from the stomach analysis in the current study.

Our results on feeding at night and digesting during the day are in accordance with Dalpadado and Gjøsæter (1987). They concluded that the skinnycheek lanternfish in the Red Sea fed less intensively after midnight. The timing of their last nocturnal trawl-haul corresponded approximately to the skinnycheek lanternfish caught at 01:00–02:00 in the current study, which also showed less intense feeding than other night-hours. However, we document increase in the stomach contents in subsequent hours between 04:00 and 06:00. In general, the frequency of fish with prey in stomachs, full stomachs and fresh stomach content increased from sunset to sunrise indicating that the skinnycheek lanternfish feed throughout the night. This is in contrast to the dusk and dawn feeding observed in some mesopelagic fish (Bagøien et al., 2001; Sabates et al., 2003), but in accordance with nocturnal feeding cycles previously observed in several lanternfish species (Holton A., 1969; Clarke, 1978; Kinzer and Schulz, 1985; Williams et al., 2001).

The Red Sea has particularly low zooplankton concentrations at mesopelagic depths (Weikert, 1982; Böttger-Schnack et al., 2008, this study). In the present study the total zooplankton abundance was <6 individuals m^{-3} within the daytime depth range of the skinnycheek lanternfish. Thus, in order to feed, the fish depend on migrating into the upper $\sim$200 m where zooplankton abundance was several hundred individuals per cubic meter. This contrasts with more productive regions where total zooplankton concentrations are higher and the amount of prey-biomass in surface-waters and mid-waters are more similar (e.g., Weikert, 1982; Sameoto, 1988; Baliño and Aksnes, 1993, this study). In such regions, lanternfishes also feed in their mesopelagic daytime habitat (Merrett and Roe, 1974; Pearcy et al., 1979; Pusch et al., 2004; Dypvik et al., 2012a), and DVM patterns appear to vary in accordance with seasonal variations in abundance and vertical distribution of prey (Dypvik et al., 2012b).

The water was slightly warmer in the surface at Atlantis II than at Kebrit, but very similar below $\sim$200 m. The uniquely warm deep-water in the Red Sea (e.g., Weikert, 1982, this study) may contribute to the complete vertical migration and the strict feeding cycle observed in the skinnycheek lanternfish population. The mesopelagic temperature of 22 °C is warmer than the temperatures lanternfishes encounter during daytime in other tropical/sub-tropical oceans, such as Hawaiian waters (e.g., Clarke, 1978; Cowles et al., 1991), the Mediterranean Sea (Olivar et al., 2012), the Gulf of Mexico (Gartner et al., 1987), and the Arabian/Oman Sea (e.g., Kinzer et al., 1993; Morrison et al., 1999), where the relevant temperatures span from $\sim$4 to 16 °C (e.g., Gartner et al., 1987; Cowles et al., 1991; Morrison et al., 1999; Olivar et al., 2012). A metabolic Q_{10} of 3.9 has been reported for lanternfishes (Donnely and Torres, 1988), a $\sim$4-fold increase per 10 °C increase in temperature. We expect that the digestion rate will increase accordingly. It appears that in the Red Sea the whole ration of prey ingested the previous night is digested in the course of the day. Thus, in accordance with the hunger/satiation hypothesis (Pearre, 2003), the level of hunger experienced by individuals and the lack of food at mesopelagic depth forces the entire population to ascend into the prey-abundant epipelagic layer to feed throughout the night.

Hypoxic levels of oxygen (<1.4 ml O_2 l^{-1} (Ekau et al., 2010)) in the mesopelagic zone of the Red Sea may affect the behavior of skinnycheek lanternfish. In extremely hypoxic waters, nocturnal ascent of fish has been attributed to alleviation of digestion suppression in hypoxic waters (Utne-Palm et al., 2010), but based on stomach content analysis, oxygen levels at both study sites in the Red Sea were sufficient for digestion within the skinnycheek lanternfish daytime depth range. In the adjacent, highly productive Arabian Sea, low oxygen levels in the mesopelagic zone are present throughout the year (Olson et al., 1993; de Sousa et al., 1996; Morrison et al., 1999). Consistent with our study, Kinzer et al. (1993) found that the entire skinnycheek lanternfish population ascended into the epipelagic layer of the Arabian Sea at night, but – in contrast to our explanation for the Red Sea – concluded that the low oxygen levels in the mesopelagic zone forced the fish to migrate into the oxygen-rich epipelagic layer at night (Kinzer et al., 1993). The same pattern seems evident in the Oman Sea (e.g., Zubkov et al., 2006; Valinassab et al., 2007). However, in another study from the Arabian Sea, Gjøsæter (1984) found that portions of the skinnycheek lanternfish population remained below 200 m throughout the night. Even though the unusual high temperatures of the Red Sea (see paragraph above) will add to the metabolic demand, the oxygen levels in the mesopelagic zone are $>93\%$ higher in the Red Sea than in the Arabian Sea (e.g., Kinzer et al., 1993; Morrison et al., 1999, this study), so we reject low oxygen concentration as a significant causative force for DVM in our study. To what extent the hypoxic oxygen levels in the Red Sea might constrain the activity level of the skinnycheek lanternfish in the mesopelagic zone (Kramer, 1987; Schurmann and Steffensen, 1992) remains to be established.

In conclusion, the skinnycheek lanternfish in the Red Sea perform NDVM, confining feeding to the upper 200 m at night, while they spend the day digesting their prey at several hundred meters depth. Light-related predation risk force the skinnycheek lanternfish to avoid the upper 200 m during daytime (Robison, 2003), while the strict daily feeding cycle is governed by the epipelagic distribution of prey, and high daytime digestion rates driven by warm temperatures at mesopelagic depths. This NDVM pattern is observed both during autumn and spring (Klevjer et al., 2012, this study), indicating that this might be a pattern present all year, possibly due to the restricted amount of seasonality in the area (e.g., no seasonal dormancy or increase of copepods in deeper waters (Weikert, 1982)). These results indicate that the skinnycheek lanternfish can be an important year-round contributor to the biological pump in the Red Sea.

Acknowledgements

We are grateful to T. A. Klevjer and A. Røstad for help during the research cruise and for processing the acoustic data. We would also like to thank R. Amundsen for processing the zooplankton samples, and the captain and crew of the R/V "Aegaeo". Finally, thanks to B. Jones and M. Berumen for helpful comments on the manuscript.

References

Antunes, A., Ngugi, D.K., Stingl, U., 2011. Microbiology of the Red Sea (and other) deep-sea anoxic brine lakes. Environ. Microbiol. Rep. 3, 416–433.

Bagøien, E., Kaartvedt, S., Aksnes, D.L., Eiane, K., 2001. Vertical distribution and mortality of overwintering *Calanus*. Limnol. Oceanogr. 46, 1494–1510.

Baird, R.C., Hopkins, T.L., Wilson, D.F., 1975. Diet and feeding chronology of *Diaphus taaningi* (Myctophidae) in the Cariaco Trench. Copeia 1975, 356–365.

Baliño, B.M., Aksnes, D.L., 1993. Winter distribution and migration of the sound-scattering layers, zooplankton and micronekton in Masfjorden, western Norway. Mar. Ecol. Prog. Ser. 102, 35–50.

Barham, E.G., 1966. Deep scattering layer migration and composition: observations from a diving saucer. Science 151, 1399–1403.

Batang, Z.B., Papathanassiou, E., Al-Suwailem, A., Smith, C., Salomidi, M., Petihakis, G., Alikunhi, N.M., Smith, L., Mallon, F., Yapici, T., Fayad, N., 2012. First discovery of a cold seep on the continental margin of the central Red Sea. J. Mar. Syst. 94, 247–253.

Böttger-Schnack, R., 1990. Community structure and vertical distribution of cyclopoid copepods in the Red Sea 1. Central Red Sea, autumn 1980. Mar. Biol. 106, 473–485.

Böttger-Schnack, R., Schnack, D., Hagen, W., 2008. Microcopepod community structure in the Gulf of Aqaba and northern Red Sea, with special reference to Oncaeidae. J. Plankton Res. 30, 529–550.
Catul, V., Gauns, M., Karuppasamy, P., 2010. A review on mesopelagic fishes belonging to family Myctophidae. Rev. Fish Biol. Fish., 1–16.
Cherel, Y., Fontaine, C., Richard, P., Labat, J.P., 2010. Isotopic niches and trophic levels of myctophid fishes and their predators in the Southern Ocean. Limnol. Oceanogr. 55, 324–332.
Clarke, T.A., 1978. Diel feeding patterns of 16 species of mesopelagic fishes from Hawaiian waters. Fish. Bull. 76, 495–513.
Collins, M.A., Xavier, J.C., Johnston, N.M., North, A.W., Enderlein, P., Tarling, G.A., Waluda, C.M., Hawker, E.J., Cunningham, N.J., 2008. Patterns in the distribution of myctophid fish in the northern Scotia Sea ecosystem. Polar Biol. 31, 837–851.
Collins, M.A., Stowasser, G., Fielding, S., Shreeve, R., Xavier, J.C., Venables, H.J., Enderlein, P., Cherel, Y., Van de Putte, A., 2012. Latitudinal and bathymetric patterns in the distribution and abundance of mesopelagic fish in the Scotia Sea. Deep Sea Res. Part 2 59, 189–198.
Cowles, D.L., Childress, J.J., Wells, M.E., 1991. Metabolic rates of midwater crustaceans as a function of depth of occurrence off the Hawaiian Islands: food availability as a selective factor? Mar. Biol. 110, 75–83.
Dalpadado, P., 1988. Reproductive biology of the lanternfish *Benthosema pterotum* from the Indian Ocean. Mar. Biol. 98, 307–316.
Dalpadado, P., Gjøsæter, J., 1987. Observations on mesopelagic fish from the Red Sea. Mar. Biol. 96, 173–183.
Dalpadado, P., Gjøsæter, J., 1988. Feeding ecology of the laternfish *Benthosema pterotum* from the Indian Ocean. Mar. Biol. 99, 555–567.
de Sousa, S.N., Dileep Kumar, M., Sardessai, S., VVSS, Sarma, Shirodkar, P.V., 1996. Seasonal variability in oxygen and nutrients in the central and eastern Arabian Sea. Curr. Sci. 71, 847–851.
Donnely, J., Torres, J.J., 1988. Oxygen consumption of midwater fishes and crustaceans from the eastern Gulf of Mexico. Mar. Biol. 97, 483–494.
Dypvik, E., Klevjer, T.A., Kaartvedt, S., 2012a. Inverse vertical migration and feeding in glacier lanternfish (*Benthosema glaciale*). Mar. Biol. 159, 443–453.
Dypvik, E., Røstad, A., Kaartvedt, S., 2012b. Seasonal variations in vertical migration of glacier lanternfish, *Benthosema glaciale*. Mar. Biol. , http://dx.doi.org/10.1007/s00227-012-1953-2.
Ekau, W., Auel, H., Pörtner, H.-O., Gilbert, D., 2010. Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macroinvertebrates and fish). Biogeosciences 7, 1669–1699.
Fotland, Å., Borge, A., Gjøsæter, H., Mjanger, H., 2000. 5. Tillegg. Håndbok for prøvetaking av fisk og krepsdyr, 3. Institute of Marine Research, Bergen 79-103.
Gartner Jr, J.V., Hopkins, T.L., Baird, R.C., Milliken, D.K., 1987. The lanternfishes (Pisces: Myctophidae) of the eastern Gulf of Mexico. Fish. Bull. 85, 81–98.
Giske, J., Aksnes, D.L., Balino, B.M., Kaartvedt, S., Lie, U., Nordeide, J.T., Salvanes, A.G.V., Wakili, S.M., Aadnesen, A., 1990. Vertical-distribution and trophic interactions of zooplankton and fish in Masfjorden Norway. Sarsia 75, 65–81.
Gjøsæter, J., 1984. Mesopelagic fish, a large potential resource in the Arabian Sea. Deep Sea Res. Part A 31, 1019–1035.
Gjøsæter, J., Tilseth, S., 1988. Spawning behaviour, egg and larval development of the myctophid fish *Benthosema pterotum*. Mar. Biol. 98, 1–6.
Godø, O.R., Patel, R., Pedersen, G., 2009. Diel migration and swimbladder resonance of small fish: some implications for analyses of multifrequency echo data. ICES J. Mar. Sci. 66, 1143–1148.
Hernandez-Leon, S., Franchy, G., Moyano, M., Menendez, I., Schmoker, C., Putzeys, S., 2010. Carbon sequestration and zooplankton lunar cycles: could we be missing a major component of the biological pump? Limnol. Oceanogr. 55, 2503–2512.
Holton, A., A., 1969. Feeding behavior of a vertically migrating lanternfish. Pac. Sci. 23, 325–331.
Kaartvedt, S., Torgersen, T., Klevjer, T.A., Røstad, A., Devine, J.A., 2008. Behavior of individual mesopelagic fish in acoustic scattering layers of Norwegian fjords. Mar. Ecol. Prog. Ser. 360, 201–209.
Kaartvedt, S., Røstad, A., Klevjer, T.A., Staby, A., 2009. Use of bottom-mounted echo sounders in exploring behavior of mesopelagic fishes. Mar. Ecol. Prog. Ser. 395, 109–118.
Kaartvedt, S., Staby, A., Aksnes, D.L., 2012. Efficient avoidance behavior causes large underestimation of mesopelagic fish biomass. Mar. Ecol. Prog. Ser. 456, 1–6.
Kinzer, J., Böttger-Schnack, R., Schulz, K., 1993. Aspects of horizontal distribution and diet of myctophid fish in the Arabian Sea with reference to the deep water oxygen deficiency. Deep Sea Res. Part 2 40, 783–800.
Kinzer, J., Schulz, K., 1985. Vertical distribution and feeding patterns of midwater fish in the central equatorial Atlantic. Mar. Biol. 85, 313–322.
Klevjer, T.A., Torres, D.J., Kaartvedt, S., 2012. Distribution and diel vertical movements of mesopelagic scattering layers in the Red Sea. Mar. Biol. , http://dx.doi.org/10.1007/s00227-012-1973-y.
Korneliussen, R.J., Heggelund, Y., Eliassen, I.K., Johansen, G.O., 2009. Acoustic species identification of schooling fish. ICES J. Mar. Sci. 66, 1111–1118.
Kramer, D.L., 1987. Dissolved oxygen and fish behavior. Environ. Biol. Fish. 18, 81–92.
Merrett, N.R., Roe, H.S.J., 1974. Patterns and selectivity in the feeding of certain mesopelagic fishes. Mar. Biol. 28, 115–126.
Moku, M., Kawaguchi, K., Watanabe, H., Ohno, A., 2000. Feeding habits of three dominant myctophid fishes, *Diaphus theta*, *Stenobrachius leucopsarus* and *S. nannochir*, in the subarctic and transitional waters of the western North Pacific. Mar. Ecol. Prog. Ser. 207, 129–140.
Morrison, J.M., Codispoti, L.A., Smith, S.L., Wishner, K., Flagg, C., Gardner, W.D., Gaurin, S., Naqvi, S.W.A., Manghnani, V., Prosperie, L., Gundersen, J.S., 1999. The oxygen minimum zone in the Arabian Sea during 1995. Deep Sea Res. Part 2 46, 1903–1931.
Olivar, M.P., Bernal, A., Moli, B., Peña, M., Ralbin, R., Castellón, A., Miquel, J., Massuti, E., 2012. Vertical distribution, diversity and assemblages of mesopelagic fishes in the western Mediterranean. Deep Sea Res. Part 1 62, 53–69.
Olson, D.B., Hitchcock, G.L., Fine, R.A., Warren, B.A., 1993. Maintenance of the low-oxygen layer in the central Arabian Sea. Deep Sea Res. Part 2 40, 673–685.
Pakhomov, E.A., Perissinotto, R., McQuaid, C.D., 1996. Prey composition and daily rations of myctophid fishes in the Southern Ocean. Mar. Ecol. Prog. Ser. 134, 1–14.
Pearcy, W.G., Lorz, H.V., Peterson, W., 1979. Comparison of the feeding-habits of migratory and non-migratory *Stenobrachius-Leucopsarus* (Myctophidae). Mar. Biol. 51, 1–8.
Pearre, S., 2003. Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. Biol. Rev. 78, 1–79.
Pusch, C., Hulley, P.A., Kock, K.-H., 2004. Community structure and feeding ecology of mesopelagic fishes in the slope waters of King George Island (South Shetland Islands, Antarctica). Deep Sea Res. Part 1 51, 1685–1708.
Robison, B.H., 2003. What drives the diel vertical migrations of Antarctic midwater fish? J. Mar. Biol. Assur. UK 83, 639–642.
Robinson, C., Steinberg, D.K., Anderson, T.R., Aristegui, J., Carlson, C.A., Frost, J.R., Ghiglione, J.F., Hernandez-Leon, S., Jackson, G.A., Koppelmann, R., Queguiner, B., Ragueneau, O., Rassoulzadegan, F., Robinson, B.H., Tamburini, C., Tanaka, T., Wishner, K.F., Zhang, J., 2010. Mesopelagic zone ecology and biogeochemistry—a synthesis. Deep Sea Res. Part 2 57, 1504–1518.
Roe, H.S.J., Badcock, J., 1984. The diel migrations and distributions within a mesopelagic community in the north east Atlantic. 5. Vertical migrations and feeding of fish. Prog. Oceanogr. 13, 389–424.
Sabates, A., Bozzano, A., Vallvey, I., 2003. Feeding pattern and the visual light environment in myctophid fish larvae. J. Fish. Biol. 63, 1476–1490.
Sameoto, D.D., 1988. Feeding of lantern fish *Benthosema glaciale* off the Nova Scotia Shelf. Mar. Ecol. Prog. Ser. 44, 113–129.
Sameoto, D., 1989. Feeding ecology of the lantern fish *Benthosema glaciale* in a subarctic region. Polar Biol. 9, 169–178.
Schurmann, H., Steffensen, J.F., 1992. Lethal oxygen levels at different temperature and preferred temperature during hypoxia of the Atlantic cod *Gadus morhua* L. J. Fish. Biol. 41, 927–934.
Shreeve, R.S., Collins, M.A., Tarling, G.A., Main, C.E., Ward, P., Johnston, N.M., 2009. Feeding ecology of myctophid fishes in the northern Scotia Sea. Mar. Ecol. Prog. Ser. 386, 221–236.
Thiel, H., 1979. First quantitative data on Red Sea deep benthos. Mar. Ecol. Prog. Ser. 1, 347–350.
Utne-Palm, A.C., Salvanes, A.G.V., Currie, B., Kaartvedt, S., Nilsson, G.E., Braithwaite, V.A., Stecyk, J.A.W., Hundt, M., van der Bank, M., Flynn, B., Sandvik, G.K., Klevjer, T.A., Sweetman, A.K., Brüchert, V., Pittman, K., Peard, K.R., Lunde, I.G., RAU, Strandabø, Gibbons, M.J., 2010. Trophic structure and community stability in an overfished ecosystem. Science 329, 333–336.
Valinassab, T., Pierce, G.J., Johannesson, K., 2007. Lantern fish (*Benthosema pterotum*) resources as a target for commercial exploitation in the Oman Sea. J. Appl. Ichthyol. 23, 573–577.
Weikert, H., 1982. The vertical distribution of zooplankton in relation to habitat zones in the area of the Atlantis II deep, Central Red Sea. Mar. Ecol. Prog. Ser. 8, 129–143.
Williams, A., Koslow, J.A., Terauds, A., Haskard, K., 2001. Feeding ecology of five fishes from the mid-slope micronekton community off southern Tasmania, Australia. Mar. Biol. 139, 1177–1192.
Zubkov, M.V., Tarran, G.A., Burkhill, P.H., 2006. Bacterioplankton of low and high DNA content in the suboxic waters of the Arabian Sea and the Gulf of Oman: abundance and amino acid uptake. Aquatic Microbiol. Ecol. 43, 23–32.